Drought mitigation by thinning

Drought mitigation by thinning: benefits from the stem to the stand along 15 years of experimental rainfall exclusion in a holm oak coppice

Authors: J. Gavinet[1], J-M Ourcival[1], J. Gauzere[2], L. García de Jalón[1], J-M Limousin[1]

1 Centre d'Ecologie Fonctionnelle et Evolutive (CEFE), Univ Montpellier, CNRS, EPHE, IRD, Univ Paul Valéry Montpellier 3, 1919 route de Mende, F-34293 Montpellier, Cedex 5, France

2 Institute of Evolutionary Biology, School of Biological Sciences, University of Edinburgh, EH93FL, UK.

Corresponding author :

Jean-Marc Limousin

Email : jean-marc.limousin@cefe.cnrs.fr

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Abstract

In northern Mediterranean forests, increasing drought stress due to the on-going climate change is combined with stand ageing due to the lack of management. Management by thinning may alleviate drought stress by reducing competition, but its application is challenging in coppices of resprouting species where its long-term consequences for tree demography and stand dynamics are difficult to evaluate. In this study, we investigate the long-term (15 years) demographic responses of holm oak (*Quercus ilex* L.) to a combination of thinning from below (-30% basal area) and experimental rainfall exclusion (-27% precipitation). Stem growth, survival and resistance to an extreme drought event were positively linked to both stem size and local competition release after thinning. Thinning improvement of growth and survival were thus due to both a selection of the biggest, most vigorous, trees and to a release of competition for water. Rainfall exclusion, on the other hand, led to a shift of the tree size-mortality relationship, which resulted in the death of bigger trees, in a faster loss of stool density and in a slower evolution of the stand basal area compared to the control. Thinning was beneficial by cancelling the rainfall exclusion effects on growth and mortality, and by doubling the stand basal area increment compared to unthinned control. The initial loss of stools due to thinning was compensated by a lower mortality, suggesting that thinning do not reduce further the amount of unique genotypes on the long-term. Positive thinning effects on stem growth decreased over time but remained significant 15 years after thinning, while resprouting dynamics strongly decreased with time. These results indicate that moderate thinning from below is a relevant strategy to increase stem vitality and stand production in old coppices, particularly in a context of a chronic rise in drought stress and more frequent extreme drought episodes.

1. Introduction

Forest ecosystems are currently facing fast changes, such as unprecedented climatic conditions and land-use changes, that already affect tree growth, mortality and reproduction (Allen et al., 2010; Doblas-Miranda et al., 2017; Linares et al., 2009; McDowell and Allen, 2015). Such changes are expected to further accelerate in the future and strongly challenge current forest management practices (Keenan, 2015; Millar et al., 2007; Stephens et al., 2010). Decreasing stand density by thinning is traditionally used to improve residual tree growth and dimensions, but it has gained a renewed interest as an adaptive management practice aiming at improving forest resistance or resilience to drought (Bottero et al., 2016; Navarro-Cerrillo et al., 2019; Vilà-Cabrera et al., 2018). By reducing stand leaf area, thinning is expected to reduce rainfall interception and stand transpiration, thereby improving water availability for the remaining trees (Bréda et al., 1995; del Campo et al., 2014; Giuggiola et al., 2015). Reduced competition for water after thinning has been shown to increase mean tree growth and to reduce growth vulnerability to extreme drought events (Aldea et al., 2017; Bottero et al., 2016), although with a high variability depending on species, climate and thinning intensity (Sohn et al., 2016b). How thinning regimes, i.e. their frequency, intensity and the characteristics of the trees harvested affect the forest resistance to drought is still poorly known. Thinning effects on tree growth and mortality strongly depend on individual characteristics such as tree size and local competitive environment (Bose et al., 2018), which also affect the drought responses (Bennett et al., 2015; Colangelo et al., 2017; Trouvé et al., 2014). Furthermore, positive thinning effects may vanish after a few years (Bréda et al., 1995; Cotillas et al., 2009; del Campo et al., 2019; Sánchez-Humanes and Espelta, 2011), and even reverse in the long-term (D'Amato et al., 2013) because stand leaf area can quickly recover to its pre-thinning values either by an increase in tree leaf area (Bréda et al., 1995; Giuggiola et al., 2013) or by the development of understory vegetation following increased light availability (Gebhardt et al., 2014; Simonin et al., 2007). Thinning is also accompanied by an increase in light, temperature and evaporative demand in the canopy and understory (Gavinet et al., 2015; Lechuga et al., 2017), possibly resulting in increased water losses by evapotranspiration that can reduce or offset thinning benefits for water availability (del Campo et al., 2019; Gebhardt et al., 2014). Moreover, when thinning reduces population sizes too strongly, genetic drift may lead to the loss of rare alleles and restrict local adaptation processes (Lefèvre et al., 2014). Thinning is thus generally considered as a short-term adaptation option (Vilà-Cabrera et al., 2018), and thinning regimes are to be determined depending on species, stand type and site conditions (Ameztegui et al., 2017; Skov et al. 2009; Sohn et al. 2016b).

Whether thinning is a suitable strategy to improve tree vitality and resistance to stress in resprouting stands is not straightforward because an important resprouting dynamic can take place after thinning and quickly offset the benefits of competition reduction (Cotillas et al., 2009; Ducrey, 1996; Ducrey and Toth, 1992). The resprouting ability allows trees to persist under disturbances or drought (Bond and Midgley, 2001; Clarke et al., 2010; Zeppel et al., 2015) and is widespread in broadleaved species such

as Mediterranean oaks. These oak forests represent the main late-successional stands around the Mediterranean basin (Quézel & Médail 2003), and because of their strong resprouting ability, they have been generally managed as coppices for the provision of fuel wood, charcoal or tannins. With rural abandonment and the decreasing use of firewood and charcoal as energy sources, oak coppices have been progressively abandoned since the middle of the XXth century and form now ageing stands with frequent signs of dieback, lack of seed regeneration and low levels of productivity (Camarero et al., 2016; Gentilesca et al., 2017). Besides, in coppice stands, the long history of coppicing has led to complex forest structures comprising both unique genets and multi-stemmed clumps (Valbuena-Carabaña et al., 2008), where individual stem growth and vigour are also influenced by stool characteristics (Salomón et al., 2013). Whether management by thinning could improve productivity and drought resistance of aged oak coppices in the long-term remains to be determined, especially in a context of climate change pushing drought stress beyond its historical range. Thinning from below at a moderate intensity, i.e. by removing the smallest suppressed stems and by keeping at least one stem on multi-stemmed stools, may limit resprouting and maintain stand-level productivity (Cabon et al., 2018b; Ducrey, 1996) as well as a large population size of unique genets. This type of thinning from below can additionally decrease fire risk by limiting the vertical continuity of the vegetation cover and limit the impact on understory temperature and evaporative demand. Thinning from below has potentially two types of effects: the selected trees are the biggest, which are often more vigorous and more efficient in resource acquisition and transformation (Binkley et al., 2004), while the removal of small trees can release the competition for belowground resources (Cabon et al., 2018b; Giuggiola et al., 2018). However, the relative importance of size-selection and competition release, the influence of stool-level variables, and the impact of thinning on genetic diversity on the long-term remain to be described in a context of increasing drought.

In this study, we investigate the effects of thinning on holm oak growth, mortality, resprouting and stool diversity under ambient and increased drought severity, by using a 15-year experiment in a mature coppice combining rainfall exclusion (-27% of incoming precipitations) and thinning from below (-30% basal area). A previous study after 5 years of treatment showed that thinning improved tree growth and survival but also increased tree resprouting, suggesting that thinning effect could be quickly offset by resprouting (Rodríguez-Calcerrada et al., 2011). Ten years later, we aimed to i) analyse the long-term evolution of thinning effects and resprouting dynamics, ii) understand the individual characteristics driving tree demographic rates (growth, survival, resprouting) and their response to drought and iii) explore the stand-level evolution of basal area, stem density and stool density – which relates to the number of unique genotypes – under the different treatments.

2. Material & method

2.1. Experimental site

The experiment was conducted in southern France (35 km northwest of Montpellier), on a flat area in the Puéchabon State Forest (43°44'29'' N; 3°35'46'' E, 270 m a.s.l.). This forest has been coppiced for centuries with clear cuts approximately every 25 years, until the last clear cut in 1942. The evergreen *Quercus ilex* L. forms a dense canopy with a height of c. 5.5 m, a mean basal area of 30 $m^2.ha^{-1}$ and a density of c. 6000 stems. ha^{-1}, representing c. 4000 genetically different individuals (stools).ha^{-1}. The evergreen species *Buxus sempervirens*, *Phyllirea latifolia*, *Pistacia terebinthus* and *Juniperus oxycedrus*, compose a sparse understory layer with c. 20% cover and represent less than 3% of stand basal area. The bedrock is a hard Jurassic limestone and the soil is extremely rocky with c. 75% of stones and rocks in the top 0–50 cm and 90% below. The stone-free fraction of the soil within the 0–50 cm layer is a homogeneous silty clay loam (38.8% clay, 35.2% silt and 26% sand). The area has a Mediterranean-type climate with a mean annual temperature of 13.2°C (on-site meteorological station, 1984-2017), the coldest month being January (5.5°C) and the hottest month July (22.9°C). The mean annual precipitation is 910 mm with a range of 550 - 1549 mm (1984-2017). Rainfall mainly occurs during autumn and winter with about 80% between September and April.

2.2 Experimental design: rainfall exclusion and thinning experiments

In March 2003, a factorial combination of throughfall exclusion and thinning treatments was set up on three 20 × 20 m replicated blocks located 200m apart one from the other. Each block comprises four treatments applied on a 10 × 10 m plot: control, throughfall exclusion (further "dry"), thinned, and thinned with throughfall exclusion (further "thinned dry"). For the throughfall exclusion treatment, half of the block was equipped with parallel 14m long and 0.19m wide PVC gutters hung below the canopy with a slope, between 1m and 2m in height, so as to cover 33% of the ground area under the tree canopy. Taking into account rainfall interception and stemflow, the net input of precipitation was reduced by 27% compared with the control plots (Limousin et al., 2008). On the other half of the blocks, identical gutters were installed upside down to homogenize albedo and understorey micro-climate without reducing precipitation inputs. Thinning from below was applied once, in winter 2003, on half of the plots by removing 30% of the initial plot basal area (27% of *Q. ilex* basal area, Table 1), thereby reducing the stem density by 49 % and stool density by 36% (Table 1). Dead, diseased and suppressed stems were felled and the understory cleared. One to four stems were cut on multi-stemmed stumps, in order to leave the larger stems. Thinning resulted in an increase of the mean *Q. ilex* stem diameter by 25% (Table 1). Measures of pre-dawn water potential on a subsample of trees during the first 5 years of the experiment confirmed that rainfall exclusion increased tree water stress while thinning decreased it (Rodríguez-Calcerrada *et al.*, 2011).

2.3 Demographic data

In each plot, stems with a diameter at breast height (DBH) larger than 2 cm were individually tagged, mapped and their DBH was measured before and after treatment application in March 2003. Neighboring trees located within a 3m band around the blocks were also measured to assess the competitive environment of the trees inside the plots. Annual inventories of stem DBH were then conducted every winter from 2004 to 2019 with a diameter tape. Annual stem basal area increments were calculated for each year n from 2003 to 2018 as $BAI_n = \frac{\pi}{4}(DBH_{n+1}^2 - DBH_n^2)$. Trees were recorded as dead when only brown leaves remained on the tree without crown regreening during the following years. Resprouts were inventoried twice, in 2008 and 2018. For each stump, the number of resprouts, the diameter of all resprouts and the height of the dominant resprout were measured. We considered the resprouts taller than 1.30m as established resprouts. None of them reached the threshold of 2cm DBH to be considered as recruits.

2.4 Stool identification and clonal structure

The stool clonal structure of the coppice was visually assessed during the first inventory by grouping as clones the stems that were visibly connected to the same stump and root system. This assessment was facilitated by the shallow and rocky soil of the site where the stumps are generally clearly visible above the ground. This visual census of genetically different individuals was then confirmed by genetic analyses performed in 2018 on a subsample of 166 individuals selected in the denser unthinned plots. Leaves were collected on one stem of every identified stump and frozen on dry ice. The DNA was extracted using DNeasy 96 Plant kit (QIAGEN GmbH, Hilden, Germany) and genotyping was performed using 70 validated SNPs markers (Bonal et al., 2019) developed from ddRAD-Seq data by the Genome Transcriptome Facility of Bordeaux (PGTB) following the methods described in García et al. (2018). To be considered clones, individuals had to be compared at more than 50 loci with exact matching of their SNP markers. The results confirmed the relative reliability of the visual assessment as only 25 individuals among the 166 sampled were unidentified clones (15% of undetected clones). The mean distance between unidentified clones was 1.05 m and never exceeded 3 m (see a map of one block in Fig. S1). These results show that stools extent was spatially restricted and that it could reliably be described from visual inventories. We therefore decided to retain the visual stool identification as a proxy for the number of genetically different individuals within the coppice.

2.5 Competition indexes

We calculated the stem-level competition index as the sum of the neighbors' basal area in a 3m radius around each stem (BAn). BAn is a distance-independent, size-symmetric competition index. Size symmetric competition occurs when each tree exerts a competitive effect proportional to its size. This is typically assumed to be the case when belowground resources such as water are the main limitation. We also computed other widely used competition indexes: two size and distance-dependent competition indexes, the Hegyi competition index (Hegyi, 1974) and the Weiner competition index (Weiner, 1984)

and the size asymmetric index Basal Area of Larger trees within a 3m radius (BAL). The models including these indexes were however always less performant than with BAn (lower or similar R^2, higher AIC, with particularly no effect of BAL, data not shown). We thus retained BAn to characterize the local competition intensity as this index is simpler and not related to tree size, allowing us to separate mechanisms of competition and size-selection. We tested the effect of competition absolute values (BAn) and competition release, expressed as the percentage of BAn removed by thinning or neighbor's mortality.

2.6 Data analysis

Annual stem basal area increment (BAI) were averaged over the 15 years of the experiment for each tree. This mean growth variable was first analysed as a function of thinning, rainfall exclusion and their interaction using a linear model. Then, we constructed a stem growth model as a function of individual characteristics using stem size in interaction with indexes of competition intensity (BAn), competition release (percentage difference of BAn before and after thinning, see above) and rainfall exclusion as explanatory variables. Thinning was not included in these latter models because it was redundant with competition indices and strongly inflated models VIF (Zuur et al., 2010). We selected the best model based on the Akaike criterion (AIC). When AIC difference between two models was lower than 2, we considered the models equivalent and selected the most parsimonious one. The variance explained by each of the predictors was assessed using the R package relaimpo (Grömping, 2006). Finally, the temporal evolution of treatment effects on tree growth was analysed by separating the dataset in three 5-years periods and analysing stem growth as a function of treatments, period and their interactions using a linear mixed model with stem identity as a random factor in order to account for repeated measures. In all models, stem growth was log-transformed to satisfy conditions of normality and homoscedasticity.

Holm oak stem and stool mortality was analysed similarly as a function of i) treatments and ii) individual characteristics. Mortality probability was modelled using a logistic regression with a logit link. Rainfall exclusion effect on the diameter of dead trees in unthinned plots was tested with a t-test.

The year 2006 had the driest spring season over the course of the experiment, with only 52mm of precipitations between April and June (average 2003 – 2018 = 211mm). Spring water limitation has been shown to be the most important environmental factor for stem growth and stand productivity in our site (Gavinet et al., 2019; Lempereur et al., 2015). We thus used data from the year 2006 to quantify the impact of an extreme drought event on individual stem growth. We calculated the drought resistance for each stem as the ratio of stem growth in 2006 to mean growth in the three preceding years (Lloret et al., 2011). Drought resistance was analyzed as described for stem BAI and mortality as a function of rainfall exclusion and thinning treatments, then as a function of individual characteristics. Drought resistance was log-transformed to obtain normal residuals and 13 outliers were discarded, corresponding

to stems with either a negative BAI in 2006 (typically due to a measurement error) or a mean BAI during the preceding years almost null, 8 of which died some years later.

Resprouts number, maximum height and total basal area per stool were analysed as a function of rainfall exclusion, thinning treatments, inventory date (5 and 15 years after thinning) and their interaction, using stool identity as a random factor to account for repeated measures. A negative binomial distribution was used for the number of resprouts to account for overdispersion (function glmer.nb of the R package lme4), and linear mixed models were used for log-transformed resprout height and basal area. When interactions between factors were significant, we performed Tukey post-hoc tests. Then, we modelled resprout basal area (the most integrative index of resprout dynamics) as a function of stool size and the percentage of stool basal area that had been cut by thinning (stool competition release).

To examine treatment effects at the stand-level, we calculated for each year and plot the relative stand basal area, stand basal area increment, stem density and stool density as the ratio of these variables to their initial values (pre-thinning). We used a linear mixed model to test the evolution of stand characteristics as a function of years since treatment application, thinning, rainfall exclusion and their interactions with plot as a random factor to account for repeated measures.

3. Results

3.1 Stem growth and resistance to drought

Mean stem growth over the 15-year period was strongly affected by thinning ($P < 0.001$, Figure 1A, explained variance of 12.2%) but not by rainfall exclusion ($P = 0.77$). Stem growth was positively related to stem DBH in interaction with stem-level competition release, so that biggest stems responded more to competition release (Table 2; Figure 1B). Stem DBH explained 53% of stem growth variance, competition release an additional 7% and the interaction between these factors 0.5%. Absolute competition (BAn) had an additive negative effect and explained 1.9% of stem growth variance.

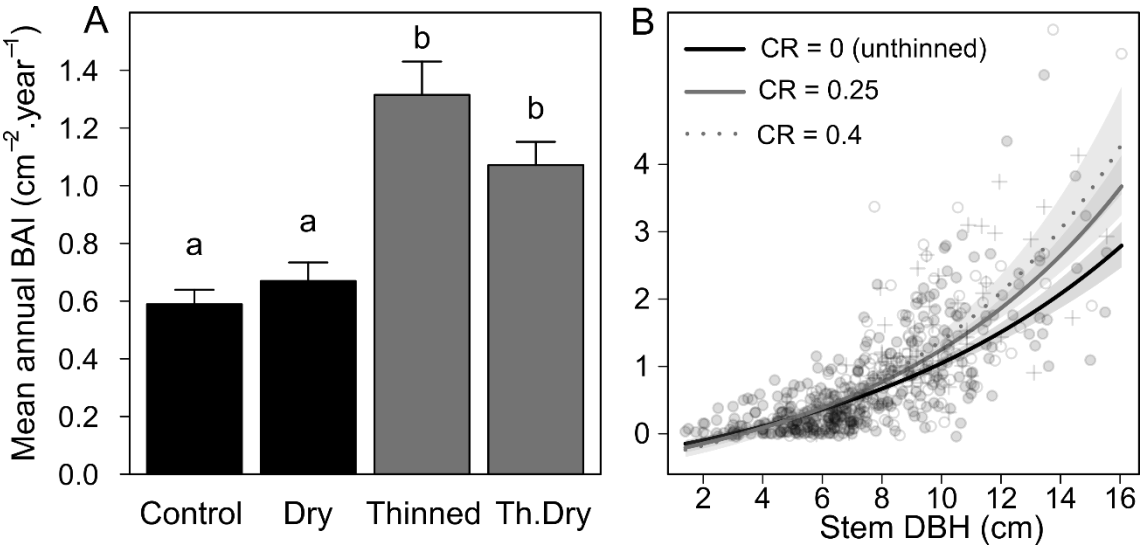
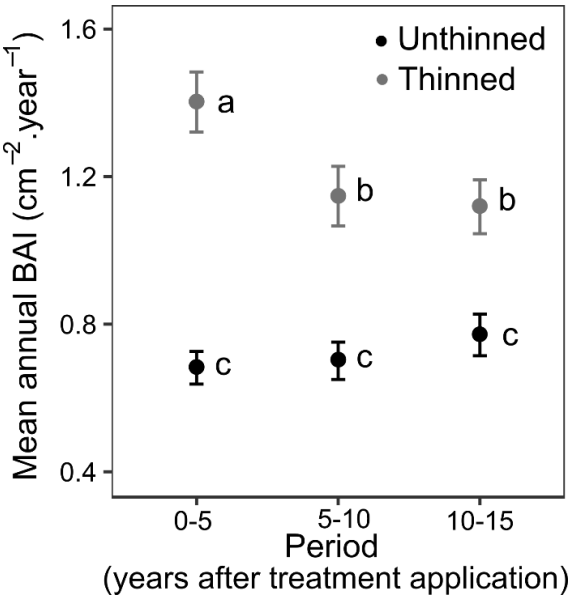


Figure 1 : *Quercus ilex* stem mean annual basal area increment (BAI) as a function of : A) treatments (means ± standard error of 99 to 173 stems per treatment, different letters indicate differences between treatments) and B) model projections and experimental data of stem BAI as a function of stem DBH and competition release (CR), confidence intervals of the models are represented in grey. CR=0 represent trees unthinned (represented by grey points), CR=0.25 is the median (white points) and CR=0.4 the upper quartile (crosses) of CR values in the thinned treatments. Point symbols are determined by the closest value of CR. Competition release is calculated as the change of neighbors' basal area in a 3m radius compared to its initial value before treatment application in 2003. Full model R^2 is 62%, stem DBH explains 53% of the variance and CR 7% (see Table 2).

Thinning effect on stem growth decreased over time (Thinning x Period interaction, $P < 0.001$; Figure 2) but remained significant ($P < 0.001$, post-hoc Tukey tests) during all the periods. Rainfall exclusion had no effect on stem growth in any of the periods (Rainfall exclusion main effect $P = 0.43$, interaction with Period $P = 0.32$).



254

255 **Figure 2:** Temporal evolution of thinning effects on *Quercus ilex* stem growth (mean ± standard
256 error). Thinning effect decrease with time but is always significant ($P < 0.001$). Different letters
257 indicate significant differences between treatments and periods (Tukey post-hoc tests).

258

259 The extreme spring drought in 2006 induced a strong reduction of stem growth to about 50% of the
260 average of the preceding years in the unthinned plots (Figure 3A). Thinning strongly increased stem
261 resistance to drought ($P < 0.001$; Figure 3) as tree growth was maintained in thinned stands. In contrast,
262 stem growth resistance to drought was not affected by rainfall exclusion ($P = 0.77$) nor by the interaction
263 between rainfall exclusion and thinning ($P = 0.25$). Thinning explained 8.1% of the variance in stem
264 growth resistance to drought. Stem resistance to drought was positively related to stem DBH (explained
265 variance = 2.5%) and competition release (explained variance = 4.5%; Figure 3B; Table 2).

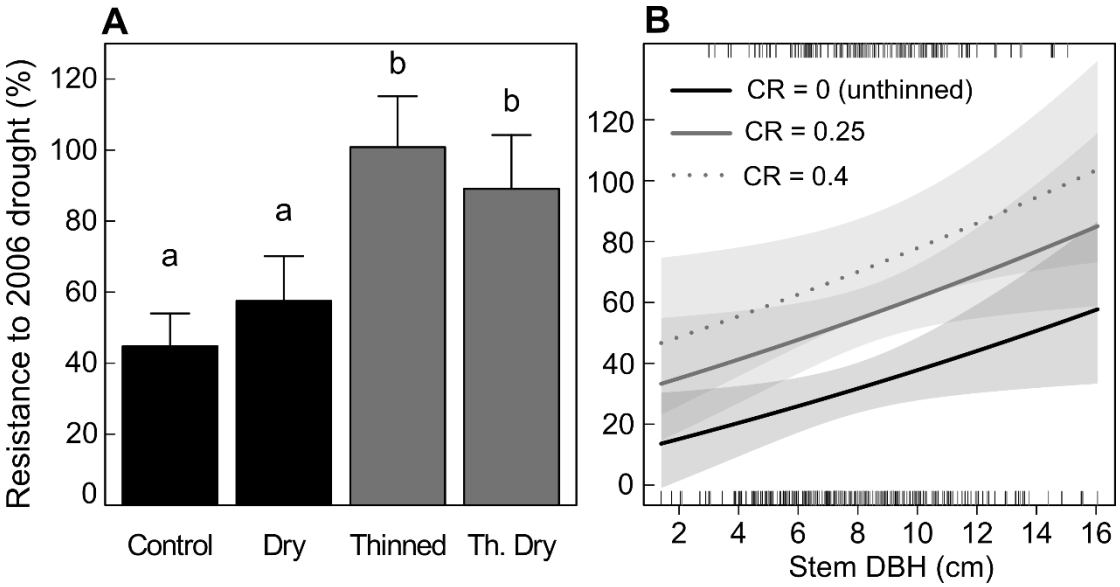
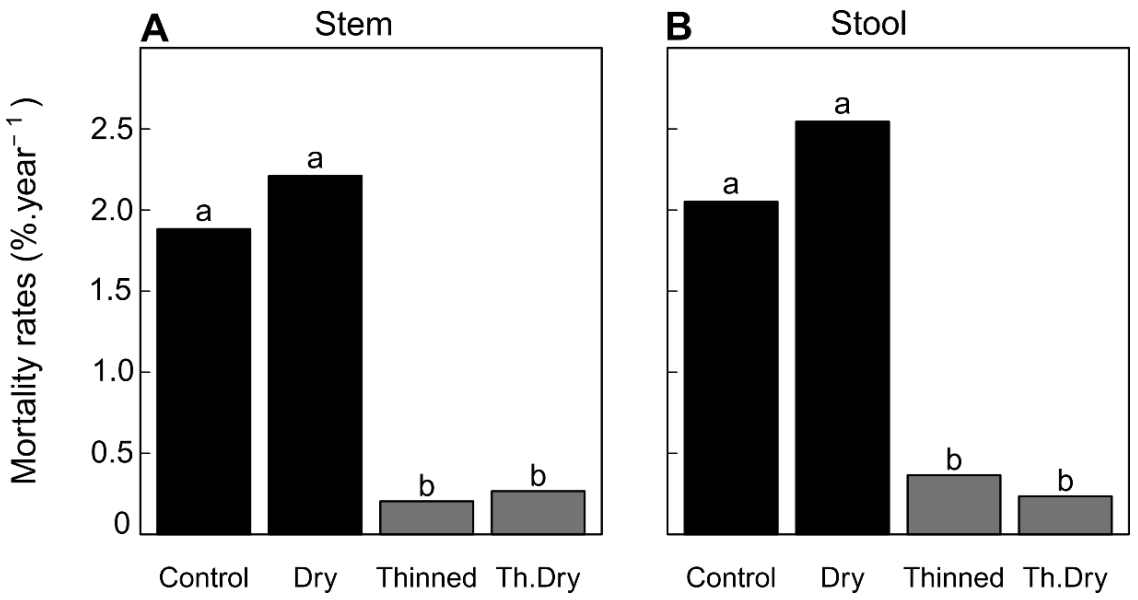


Figure 3 : *Quercus ilex* stem growth resistance to the extreme 2006 drought as a function of A) treatments (means ± standard error of 85 to 123 trees per treatment) and B) model projections of drought resistance as a function of stem DBH and competition release (CR) with confidence intervals in grey and ticks representing data distribution. Full model R^2 is 7%, stem DBH explains 2.5% of the variance and CR 4.5% (see Table 2).

3.2 Stem and stool mortality

The average stem mortality rate was 2.2%.year^{-1} in control stands and was not significantly increased by rainfall exclusion ($P = 0.14$). The mortality rate was, however, strongly decreased to only 0.2%.year^{-1} in thinned stands ($P < 0.001$, explained variance of 18%): only 3 and 4 stem deaths were recorded in thinned and thinned dry stands, respectively. Similarly, at the stool-level, the mortality rate was 2.1%.year^{-1} in the control stands and increased to 2.5%.year^{-1} in the dry treatment, although this difference was not significant ($P = 0.22$). Thinning strongly reduced stool mortality ($P < 0.001$) to 0.03%.year^{-1}, regardless of the rainfall exclusion treatment (Figure 4B).



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283 **Figure 4** : *Quercus ilex* stem (A) and stool (B) annual mortality rates as a function of treatment.
284 Different letters indicate differences between treatments ($P< 0.05$).

285

286 Stem mortality probability was influenced by stem DBH, competition release and rainfall exclusion
287 (Table 2, Figure 5). Stem mortality risk was higher for smaller stems: all trees under 3 cm of DBH died
288 during the 15 years of the experiment while the mortality probability was almost null for DBH higher
289 than 10 cm. Stem DBH explained 40% of the variance of the mortality risk, rainfall exclusion 4% and
290 competition release 4%. Taking into account stem diameter, the mortality risk was higher in the dry
291 treatment (P=0.003, Table 2) and decreased with competition release. The mean diameter of dead stems
292 was higher in the rainfall exclusion treatment in unthinned plots (t = -3.16, P = 0.002, Figure 5A). The
293 stool mortality risk was also higher for smaller stools, and rainfall exclusion shifted the mortality risk
294 toward bigger stools in the unthinned treatment (Rainfall exclusion x Stool BA, P = 0.01, Supp. Figure
295 S2).

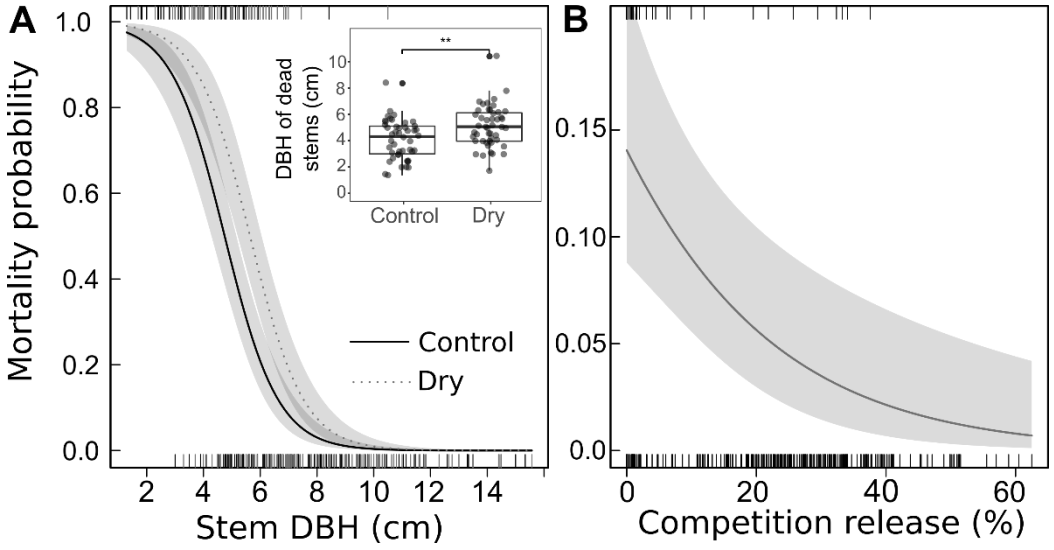
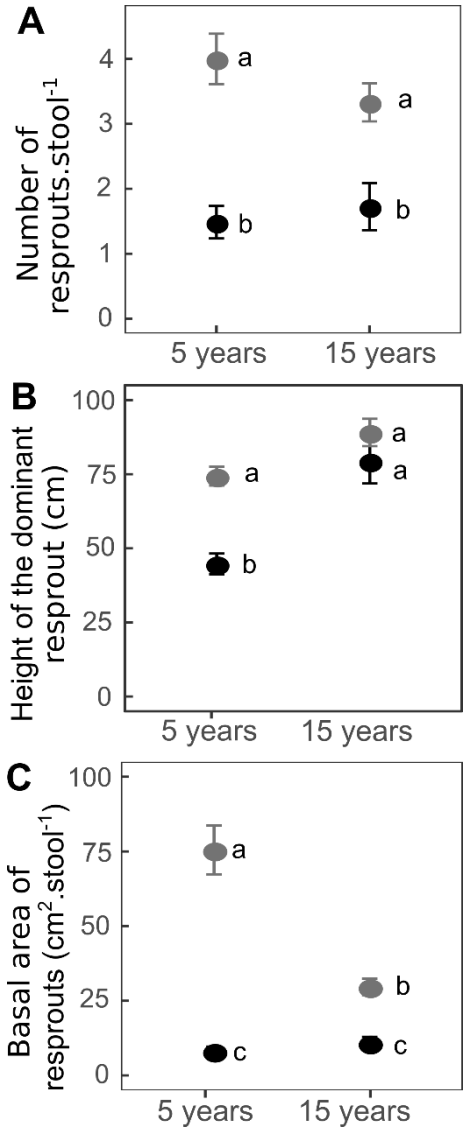


Figure 5 : *Quercus ilex* stem mortality probability as a function of A) stem DBH and rainfall exclusion treatment - the inset shows dead stems DBH as a function of rainfall exclusion treatment in unthinned stands, asterisks denote the significance of a t-test (**, $P < 0.01$) - and B) competition release, for a median DBH value (7.3 cm). Grey areas represent the confidence intervals of the models. Ticks represent dead (top) and alive (bottom) trees according to their DBH and rainfall exclusion treatment (black = Control, grey = Dry). Full model R^2 = 48% (variance explained by stem DBH 40%, Rainfall exclusion 4% and Competition release 4%).

3.3 Resprouting dynamics

None of the resprouts characteristics was influenced by rainfall exclusion (Table S1). Resprouts number was higher in thinned plots at the two inventory dates (Table S1, Figure 6A). Resprouts maximal height was higher in thinned plots after 5 years but did not differ among treatments after 15 years (Table S1, Fig 6B). The established resprouts (height > 1.30m) after 15 years represented 22% of the resprouts in thinned plots and 13% in unthinned plots. Resprouts basal area was higher in thinned plots in both inventory dates, but it strongly decreased between the two inventory dates in thinned stands resulting in a lower difference between treatments after 15 years (Table S1, Figure 6C). Resprouts basal area increased with stool size ($P < 0.001$) and with the proportion of stool basal area cut ($P < 0.001$), with a positive interaction between these two factors ($P < 0.001$) so that stool size influenced less the resprouting when it had not been thinned (data not shown).



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317 **Figure 6**: *Quercus ilex* resprouts number per stool (A), height of the dominant resprout (B) and total
318 basal area of the resprouts (C) as a function of thinning treatment (black: unthinned, grey:
319 thinned) and period. Data are means ± standard error of 246 to 284 stools per thinning treatment
320 (pooled over the rainfall exclusion treatment which had no effect). Different letters indicate
321 differences between treatments and inventory date ($P < 0.005$, Tukey post-hoc tests)

322

323 *3.4 Evolution of the stand basal area and density*

324 Stand basal area increment was 0.16 ± 0.05 $m^2 \cdot ha^{-1} \cdot year^{-1}$ in the control plots and decreased to 0.06 ±
325 0.07 $m^2 \cdot ha^{-1} \cdot year^{-1}$in the dry plots, although the difference was not significant ($P = 0.3$). Stand basal
326 area increment was more than doubled in thinned stands, up to 0.41 ± 0.06 $m^2 \cdot ha^{-1} \cdot year^{-1}$ (difference
327 from the control : $P<0.001$), with no significant decrease under drier conditions (0.39 ± 0.06 $m^2 \cdot ha^{-1} \cdot year^{-1}$, Table 3). Since the start of the experiment, a net annual loss of basal area (when mortality

329 exceeds the growth of the remaining stems) occurred in 3 years in the control plots and in 7 years in the
330 dry plots but never occurred in thinned plots.

331 The relative basal area (as the percentage of plot initial basal area) was strongly influenced by the
332 interaction between time, rainfall exclusion and thinning (P = 0.001, Table 3). In the unthinned
333 treatments, rainfall exclusion led to a slower progression of stand basal area (0.3 vs 0.8%.year^{-1}; Figure
334 7A). After the initial reduction of basal area due to thinning, the increase in basal area was much faster
335 in thinned stand, reaching 1.4%.year^{-1} with no difference between the thinned and thinned dry plots. The
336 differences between thinned and unthinned plots thus progressively decreased over time: after 15 years
337 thinned stands had recovered about 95% of their initial basal area.

338 Stem and stool relative density were both influenced by the 3-way interaction between time, thinning
339 and rainfall exclusion (Table 3). Stem and stool densities decreased faster in the dry (slopes of -1.8 and
340 -2.1 %.year^{-1}, respectively) than in the control treatment (slopes of -1.3 and -1.5%.year^{-1}). In the thinned
341 treatments, after an initial reduction of stem and stool densities by about 50% and 36% due to thinning,
342 they remained stable in time (slope not different from 0) in both thinned and thinned dry plots. At the
343 end of the experiment, stem density was still higher in the unthinned plots (Figure 7B), but from 2010
344 (after 7 years of treatment) stool density was not significantly different between thinned and unthinned
345 plots (Figure 7C).

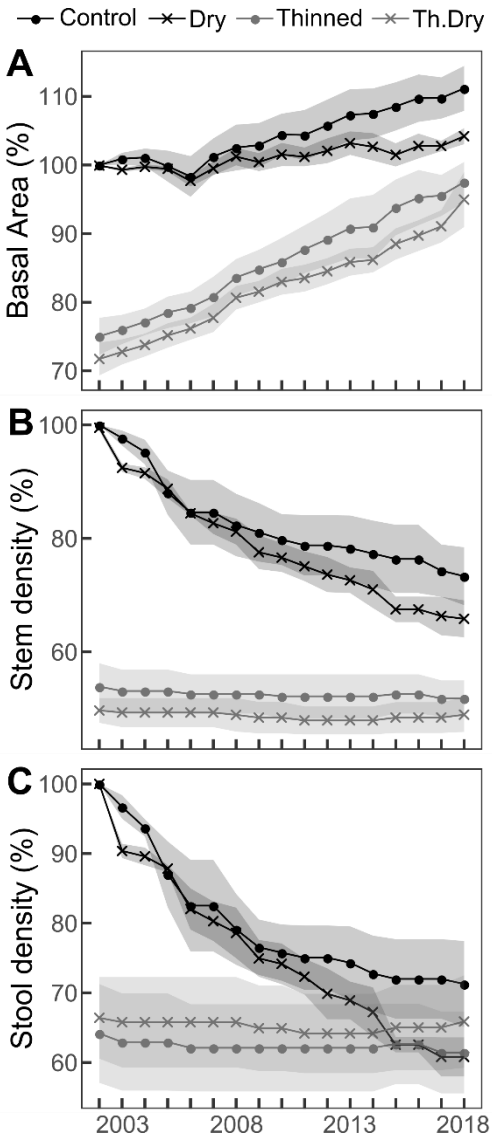

Figure 7: Evolution of *Quercus ilex* relative stand basal area (A), stem density (B) and stool density (C) as a percentage of pre-thinning values in the different treatments. Data are means ± standard error of 3 plots per treatment.

4. Discussion

4.1 Thinning and rainfall exclusion effects from the stem to the stand

Thinning strongly stimulated stem growth and increased the resistance to an extreme drought event, thereby confirming the interest of this management practice to alleviate drought effects on stem growth (Cabon et al., 2018b; Navarro-Cerrillo et al., 2019; Sohn et al., 2016b). Partial rainfall exclusion, in contrast, had no effect on individual stem growth, probably because growth occurs mainly during spring rainy periods when the difference in tree water stress between rainfall exclusion treatments is low (Gavinet et al., 2019; Rodríguez-Calcerrada et al., 2011), and also because of a change in tree allocation in favor of wood compared to leaves and fruits (Gavinet et al., 2019). The rainfall exclusion effect

appeared, however, as a shift of the size – mortality risk relationship toward the bigger individuals, which led to more frequent losses of basal area and consequently a slower basal area increment at the stand-level. In thinned stands, mortality was almost completely cancelled which, combined with the faster growth, resulted in a stand basal area increment more than doubled compared to the control, similarly to what was observed by Ogaya et al. (2019) in another *Q. ilex* stand. In our experiment, thinning proved to have larger effects on stem growth and mortality than rainfall exclusion, in line with recent studies at larger scales showing that competition is more important than climate in determining forest demography (Fernández-de-Uña et al., 2015; Ruiz-Benito et al., 2013; Zhang et al., 2015).

The loss of stools from mortality appeared to happen faster than the loss of stems in the unthinned plots, and this tendency was reinforced by the rainfall exclusion. The consequence of this phenomenon is a progressive loss of unique genotypes within the coppice stand and an increasing level of clonality (ratio of stems overs stools), especially under more stressful dry conditions. This result suggests that multi-stemmed stools survive better to the increased competition for water under rainfall exclusion (Fig. S2), either because they grow in more favourable micro-habitats or because these individuals are better genetically adapted to drought. Thinning, on the other hand, reduced the initial stool density in the plots by 36%, but our experiment revealed that thinning maintained population sizes and did not induce further loss of unique genotypes in the long-term. Interestingly, all treatments converged toward a similar stool density by the end of our 15-year study. Drastic reductions in the number of unique genotypes (by thinning and/or mortality) can lead to the loss of rare alleles (Danusevicius et al., 2016). However, previous studies have shown that moderate thinning intensities have rather limited consequences on genetic diversity in the long-term (Danusevicius et al., 2016; Koskela et al., 2013; Valbuena-Carabaña et al., 2008). On the contrary, thinning has been shown to increase acorn production in our experimental site (Gavinet et al., 2019), so it may result in positive effects on sexual regeneration and seedling diversity (Lefevre et al., 2014).

4.2 Stem performances and thinning effects are linked to stem size and competition release

Stem size had a strong positive effect on stem growth, probability of survival and, to a lesser extent, growth resistance to drought. The strong decrease in mortality risk with tree size has been often evidenced in Mediterranean forests (Colangelo et al., 2017; Hülsmann et al., 2017; Ruiz-Benito et al., 2013) but contrasts with results from more humid forests (Bennett et al., 2015). This positive effect of stem size on all stem performances may be linked to a better access of big trees to deep water (Kerhoulas et al., 2013) and suggests that this holm oak stand, even 70 years after the last clear-cut, is still in a self-thinning dynamic where suppressed stems are more likely to die while dominant trees are still vigorous. By selecting the biggest, most vigorous stems, thinning from below directly improved the mean stem growth, survival and resistance to drought. Thinning thus anticipated the self-thinning: we can estimate that about 60% of the stems and all the stools that have been cut would have died during the following 15 years (see Table 1; Figure 6b; Appendix. S2). This size-selection effect accounted for about half of

the thinning effect on stem growth. Conversely, the fact that rainfall exclusion limited the positive influence of stem or stool size on the mortality risk could indicate a deeper depletion of water resources in the dry treatment.

Thinning effects on stem growth were stronger for bigger stems, which were more able to respond to competition release. A similar disproportionate effect of thinning on the bigger stems has previously been found for *Q. ilex* (Cabon et al., 2018b; Mayor and Rodà, 1993), and for *Q. faginea* (Cañellas et al., 2004), while on boreal species Bose et al. (2018) found that tree size had no influence on the thinning response and (Jones et al., 2009) that small trees responded more. In our experiment, thinning was made from below by removing only the smallest stems so the increase in light availability was very limited for the bigger, dominant trees. Competition release, that explained roughly half of the thinning effects on stem growth and resistance to drought, is thus probably related to a release of competition for water. Competition for water is indeed more symmetric than competition for light (Schwinning and Weiner, 1998), so that the suppression of small trees or even of understory shrubs can increase water availability for big trees (Giuggiola et al., 2018). The stronger effect of competition release on bigger trees suggests that they had a greater capacity to expand their root system to take up this additional water. Kerhoulas et al. (2013) observed that bigger trees, but also trees growing in thinned stands, rely on deeper water sources than small trees or trees in denser stands, suggesting that thinning indeed foster root expansion. In addition, the higher relative importance of competition release compared to stem size for resistance to an extreme drought event also points to the improvement of water availability as the main mechanism for thinning effects during an extreme drought. This improvement of water availability may arise both from a deeper rooting and from a decrease in stand-level transpiration (Gavinet et al., 2019), delaying the depletion of water resources in thinned stands (Cabon et al., 2018b).

Remarkably, absolute values of local competition index had less influence on stem growth than competition release. Given that the stand history is homogeneous, the low explanatory power of neighbor basal area may reflect the fine-scale spatial heterogeneity of the soil rock fraction and water holding capacity. Indeed, in this very rocky soil, a low value of neighbor basal area probably reflects bad local conditions because the vegetation is expected to be in equilibrium with the local soil carrying capacity (Cabon et al., 2018a; Eagleson, 1982). Absolute values of neighbor basal area after thinning are thus a poor predictor of competition intensity, as these values already differed before thinning due to soil heterogeneity. Interestingly, this may suggest that the same percentage of basal area removal could be applied successfully across variable local soil conditions, although this remain to be assessed in a more variable context.

4.3 Temporal evolution of treatment effects

Thinning effect on tree growth decreased with time as expected, but it remained positive 15 years after thinning even though the stand almost recovered its initial basal area. This long lasting thinning effect

contrasts with studies in temperate forests where thinning effect can vanish in a few years (e.g. Bréda et al., 1995). Slow growing species such as *Q. ilex* take longer to recover to their pre-thinning basal and leaf area. In line with this idea, Bose et al. (2018) also observed that thinning effects lasted longer for shade-tolerant species. In Mediterranean forests, thinning effects were observed to be maintained to a similar level after 8 years in a *Q. faginea* stand (Cañellas et al., 2004) and to remain significant after 12 years in a *Q. ilex* stand (Mayor and Rodà, 1993) and after 20 years in *Pinus halepensis* stands (Manrique-Alba et al. 2020). In contrast, in a mixed stand including *Q. ilex* and *Q. faginea*, Cotillas et al. (2009) found that growth stimulation after thinning vanished after only 2 years and attributed this to a fast and intense resprouting in their low-density stand. Here, resprouting was rather intense in the first years after thinning (Figure 5; Rodríguez-Calcerrada et al., 2011), particularly for big stools that had been intensively cut as resprouting is known to be stimulated by previous stool size and thinning intensity (e.g. Adamec et al., 2017). We then observed a decrease over time in resprouts number and summed basal area in the thinned plots, meaning that resprout mortality was not compensated by resprout growth probably because the thinning from below did not increase sufficiently light availability in the understory. This contrasts with results by Retana et al. (1992) who observed that the decreasing number of resprouts was compensated by their increasing size, so that the total biomass of resprouts remained constant over time. Besides, no vegetative recruits were produced in the 15-year period following thinning in our study. This confirms that our low-intensity thinning from below was effective at controlling the resprouting dynamic in thinned stands, which probably participates in explaining the long-lasting effects of thinning in our site.

As a consequence of this absence of recruitment and of the self-thinning mortality in unthinned stands, stool densities are now similar in thinned and unthinned stands, and stand basal area is expected to become similar in the coming years. In the future, both stands will thus converge to similar structures, but generated either by management or by natural mortality. If drought sensitivity is partly genetically determined, then natural mortality may select for the best adapted trees. On the contrary, thinning may relax this selection and lead to maladaptive responses on the long-term, questioning the relevance of such management for forest adaptation to climate change (Lefevre et al. 2014). Once competition release has been offset by the growth of neighbors, frequent thinning may be needed to maintain positive effects on drought responses (Sohn et al., 2016a). Here, the positive thinning effect on growth resistance to drought has been highlighted only 3 years after thinning application and remains to be confirmed for further extreme drought events. In our experiment, thinning removed the small trees that proved to be more sensitive to drought in terms of growth and mortality, and has probably fostered root expansion, which may also induce long-term positive effects on drought resistance. Whether this will be enough to sustain an improved resistance to drought on the long-term, or whether natural mortality does a better job in selecting for drought resistance, remain to be assessed in the future decades.

5 Conclusion and implications for management

This ageing oak coppice was still in a self-thinning phase 70 years after the last clear-cut, with a progressively decreasing number of individuals and a low stem and stand-level growth. Long-term increased drought by experimental rainfall exclusion led to the death of bigger trees than in the control treatment, which slowed the stand basal area increment. Thinning from below can cancel the drought effects by stimulating stem growth and avoiding mortality, even under chronic or extreme drought. The basal area increment at the stand level was twice faster in the thinned stand, while the loss of unique genotypes was not larger in the long-term than the one induced by natural mortality. Size-selection of the most vigorous stems and competition release for belowground resources both participate to explain thinning effects. Positive thinning effects diminished over time but remain significant after 15 years. By applying a moderate thinning intensity (-30%), keeping the dominant tree layer and keeping at least one stem on multi-stemmed stool, resprouting dynamic was rather limited, which may have participated to the long-lasting thinning effects and is important for fire prevention. A test of this thinning regime in other stands with differing climatic and edaphic conditions is required to confirm its benefits under a wide range of situations. Thinning has also been shown to improve stand-level above-ground productivity and fruit production while reducing water consumption (Gavinet et al., 2019), thus confirming that it can be an efficient way to improve stand and tree vitality and to adapt the Mediterranean coppices to climate change. Thinning oak coppices will also result in forests with bigger trees, which may be used for other products than traditional fuel wood.

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Tables

Table 1 : Stem, stool and stand characteristics before and after thinning. Means and range (within brackets) of the different metrics are shown. BA = Basal Area. Neighbors basal area is calculated within a 3m-radius circle around each stem.

	DBH (cm)	**Neighbors BA** (cm^2/m^2)	**Stool BA** (cm^2)	**Plot BA** (m^2/ha)	**Stem density** (nb/ha)	**Stool density** (nb/ha)
Control	6.6 [1.3 - 15.3]	25.9 [6.1 - 53.6]	69.9 [1.6 - 531.4]	24.2 [23.4 – 25.1]	5767 [4000 - 6900]	3470 [1700 -4500]
Dry	7.2 [1.7 - 15.6]	26.8 [9.6 - 57.0]	76.2 [4.1 - 701.7]	27.6 [22.4 - 31.0]	6133 [5100 - 7000]	3630 [3300 -4200]
Thinned	7.2 [1.0 - 15.7]	26.3 [4.5 - 46.5]	70.6 [0.7 - 706.2]	27.9 [19.6 – 32.6]	5867 [4000 - 8000]	4030 [2600 - 5900]
Thinned Dry	6.6 [1.2 - 13.5]	26.3 [6.2 - 41.3]	70.5 [1.1 - 453.7]	29.7 [22.5 - 36.4]	6933 [6000 - 8100]	4230 [3500 - 5000]
After thinning						
Thinned	9.0 [4.0 - 15.7]	20.1 [3 -34.6]	86.8 [12.9 - 486.0]	20.8 [15.9 – 23.5]	3133 [2400- 3900]	2470 [1700 - 3200]
Thinned Dry	8.3 [2.2 - 13.5]	19.0 [4.3 - 31.7]	77.4 [7.1 -393.3]	21.9 [16.9 - 25.1]	3433 [3200 - 3600]	2830 [2600 - 3100]
After 15 years						
Control	8.5 [3.4 - 16.4]	32.0 [6.3 – 64.5]	112 [11.3 - 622]	27 [26.2 – 28.2]	4167 [3400 – 4900]	2400 [1500 - 2900]
Dry	9.2 [3.7 - 17.1]	30.7 [9.1 – 51.0]	128 [13.9 - 802]	28.9 [23.6 – 31.7]	4133 [3000 – 4900]	2230 [1900 - 2600]
Thinned	10.5 [4.8 - 18.9]	28.4 [3.7 – 47.2]	117 [18.1 - 654]	26.6 [21.1 – 29.7]	3033 [2300 – 3600]	2267 [1600 - 2800]
Thinned Dry	9.7 [3.6 - 15.2]	25.9 [7.3 – 45.1]	102 [24.4 -541]	27.9 [22.7 – 32.2]	3300 [3100 – 3400]	2733 [2500 - 3000]

Table 2: Parameters of the best individual model for stem growth, growth resistance to drought and mortality risk. See model predictions on Figure 1B, 3B and 5.

Stem growth - log(BAI+1), $cm^2.year^{-1}$			
	Estimate	Standard error	*P* - value
Intercept	-0.21	0.05	<0.001
DBH	0.10	0.005	<0.001
Competition Release (CR)	-0.38	0.25	0.14
DBH:CR	0.08	0.03	0.01
Basal Area of the neighbors (BAn)	-0.004	0.002	0.02
r^2	*0.62*		
Stem resistance to drought – $\log(BAI_{2006}/\text{mean}(BAI_{2003},BAI_{2004},BAI_{2005}) +1)$			
Intercept	0.09	0.08	0.2
DBH	0.02	0.01	0.02
Competition Release (CR)	0.64	0.15	<0.001
r^2	*0.07*		
Mortality probability – log odds (mortality)			
Intercept	4.9	0.6	<0.001
DBH	-1.04	0.11	<0.001
Competition Release (CR)	-4.87	1.55	0.1
Rainfall exclusion	0.8	0.3	0.003
Pseudo-r^2	*0.48*		

Table 3: Results of the linear mixed model analysis for stand-level evolution of basal area increment, relative basal area, relative stem density, and relative stool density (as a fraction of initial situation at the start of the experiment in 2003) according to time and treatments. Significant P-values are highlighted in bold.

		Basal Area Increment		Relative Basal Area		Relative Stem Density		Relative Stool Density	
	DF	F	*P* - value	F	*P* - value	F	*P* - value	F	*P* - value
Rainfall Exclusion (E)	1	1.3	0.28	2.43	0.16	1.5	0.25	**0.03**	0.86
Thinning (Th)	1	31.1	**<0.001**	58.8	**<0.001**	72.8	**<0.001**	6.3	**0.03**
Time (Ti)	15	0.9	0.35	1415.3	**<0.001**	528.9	**<0.001**	426.3	**<0.001**
E × Th	1	0.6	0.44	0.01	0.94	0.01	0.92	0.6	0.47
E × Ti	15	0.1	0.76	31.1	**<0.001**	11.49	**<0.001**	11.3	**<0.001**
Th × Ti	15	0.6	0.43	263.1	**<0.001**	440.7	**<0.001**	370.5	**<0.001**
E × Th × Ti	15	0.1	0.92	12.125	**0.001**	11.14	**0.001**	10.7	**0.001**

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729 **Supplementary material**

730

731 **Table S1** : Resprouts characteristics according to treatments and inventory date : ANOVA Table. Significant *P*-values are highlighted in bold.

732

	D.F.	**Number of resprouts per stool**		**Height of the dominant resprout**		**Basal Area of resprouts per stool**	
		LR χ^2	P	LR χ^2	P	LR χ^2	LR χ^2
Rainfall exclusion (E)	1	1.8	0.17	0.1	0.7	1.4	0.23
Thinning (T)	1	50.1	**<0.001**	23.1	**<0.001**	84.4	**<0.001**
Inventory date (D)	1	1.4	0.24	19.2	**<0.001**	1.5	0.22
E × T	1	1.2	0.28	0.7	0.38	0.4	0.51
E × D	1	0.8	0.37	0.5	0.48	0.6	0.44
T × D	1	0.9	0.33	9.4	**0.002**	4	**0.04**
E × T × D	1	0.01	0.95	2.3	0.12	0.03	0.86

733

Figure S1 : Map of one experimental block showing the spatial aggregation patterns of stems and stools. Each stem is a point (or a triangle for secondary species) and the first number represents the stool number followed by the stem number within the stool (#stool_#stem). Stems cut by thinning and dead stems in 2018 are also indicated

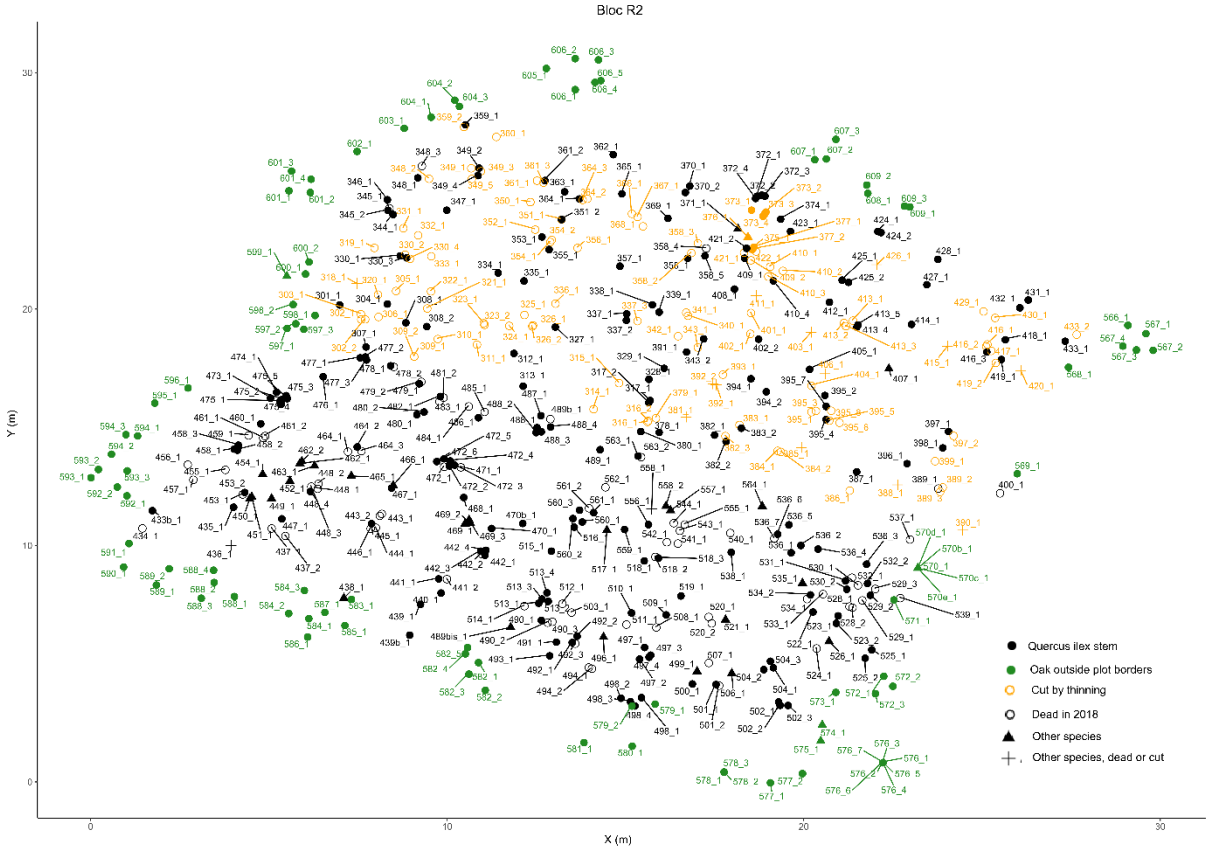
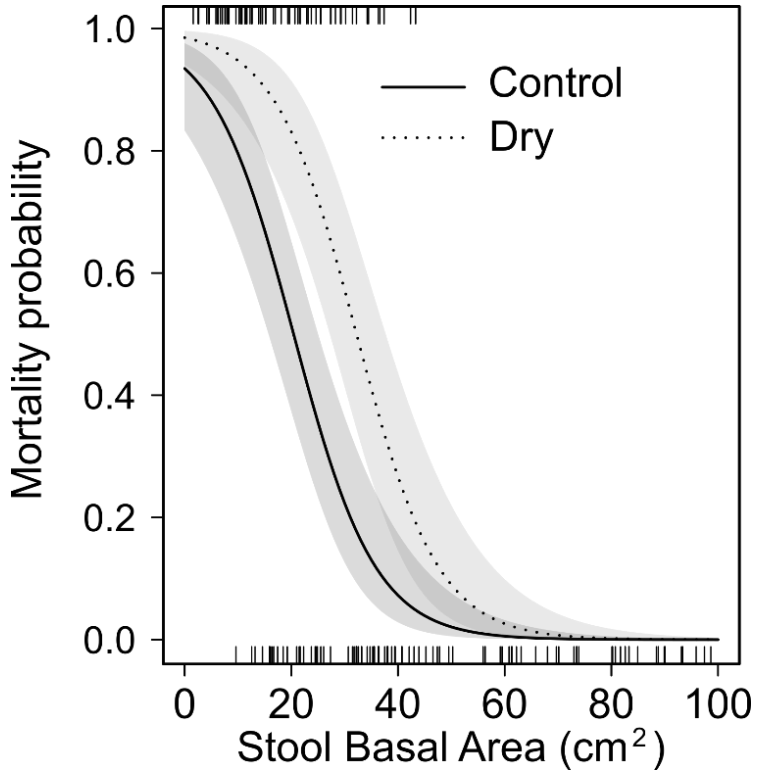


Figure S2 : *Quercus ilex* stool mortality probability as a function of stool basal area and rainfall exclusion treatment. Grey areas indicate confidence intervals of the model.


Mortality probability
1.0
0.8
0.6
0.4
0.2
0.0
Control
Dry
0
20
40
60
80
100
Stool Basal Area (cm^2)

741